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RESEARCH PAPER

The fate of ^{15}N-labeled nitrogen inputs to pot cultured beech seedlings

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Abstract: The partitioning of nitrogen deposition among forest soil (including forest floor), leachate and above- and belowground biomass of pot cultured beech seedlings in comparison to non-cultured treatments were investigated by adding 1.92 $g \cdot m^{-2}$ ^{15}N tracer in throughfall for two successive growing seasons at a greenhouse experiment. Ammonium and nitrate depositions were simulated on four treatments (cultured and non-cultured) and each treatment was labeled with either ^{15}N-NH_4^+ or ^{15}N-NO_3^-. Total recovery rates of the applied ^{15}N in the whole system accounted for 74.9% to 67.3% after ^{15}N-NH_4^+ and 85.3% to 88.1% after ^{15}N-NO_3^- in cultured and non-cultured treatments, respectively. The main sink for both ^{15}N tracers was the forest soil (including forest floor), where 34.6% to 33.7% of ^{15}N-NH_4^+ and 13.1% to 9.0% of ^{15}N-NO_3^- were found in cultured and non-cultured treatments, respectively, suggesting strong immobilization of both N forms by heterotrophic microorganisms. Nitrogen immobilization by microorganisms in the forest soil (including forest floor) was three times higher when ^{15}N-NH_4^+ was applied compared to ^{15}N-NO_3^-. The preferential heterotrophic use of ammonium resulted in a two times higher retention of deposited ^{15}N-NH_4^+ in the forest soil as compared to plants. In contrast, nitrate immobilization in the forest soil was lower compared to plants, although statistically it was not significantly different. In total the immobilization of ammonium in the plant-soil system was about 60% higher than nitrate, indicating the importance of the N-forms deposition for retention in forest ecosystems.

Keywords: ^{15}N tracer; nitrogen retention and recovery; beech seedling; forest soil; immobilization; nitrogen budget

Introduction

Temperate forests are recipients of anthropogenic nitrogen deposition. It is demonstrated that elevated atmospheric N inputs to forest ecosystems in long term can lead to increased net N mineralization and nitrification in soils, increased soil acidification, nutrient imbalances in plant tissues, reductions in plant growth, changes in species composition, altered fluxes of trace gases and increased nitrate leaching and simultaneous base cations losses (Aber et al. 1989; Bowden et al. 1991). The excessive nitrogen inputs have led to concerns regarding the ability of forest ecosystems to assimilate and retain additional nitrogen and saturation of nitrogen retention capacity in forest ecosystems with respect to nitrogen inputs (Aber et al. 1989; Aber 1992; Durka et al. 1994; Wright and Van Breemen 1995; Dise and Wright 1995). Because growth in forest ecosystems is often limited by N availability, elevated N inputs from the atmosphere can influence above- and belowground biomass production in forests. The assimilation of N by vegetation is small relative to the quantity of N retained by soil organic matter (Aber et al. 1993; Nadelhoffer et al. 1995; Magill et al. 1996, 1997, 2000). The processes by which N retention and incorporation occur in total plant-soil system and the effect of added N on soil nitrogen cycling dynamics are not well understood. Many important transformations of nitrogen within the soil system are microbially driven including immobilization and mineralization of N during decomposition. Gundersen et al. (1998) argued that although forest soils may have a large capacity to retain N, changes in the vegetation and forest floor were sufficient to change the functioning of the N cycle and result in NO_3^- leaching. Thus, the ability to predict N saturation will require a quantitative understanding of the rates of internal cycling within the plant, forest floor, and within the plant-soil cycle. The application and recovery of ^{15}N enriched tracers in forests has proven to be a powerful tool for gaining insight into N fluxes and transformations in soils (Davidson et al. 1990; Tietema and Wessel 1992) and vegetation (Preston et al. 1990).

The present study contributes to the discussion regarding the function of the forest soil in nitrogen transformation of forest ecosystems. Tracing the two N forms within an ecosystem using ^{15}N is advantageous because the system natural N level is relatively unaltered. Furthermore, because N deposition in north temperate regions ranges from <2 $kg \cdot ha^{-1} \cdot a^{-1}$ to >50 $kg \cdot ha^{-1} \cdot a^{-1}$

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(Galloway et al. 1995), it is important to determine whether assimilation of N inputs into forest ecosystem pools varies with N inputs. Therefore, we used ^{15}N tracer additions to experimental plots to address the following questions. (1) What are the dominant sinks for N deposition in forests under beech seedlings plantation? (2) Does the ionic form of N deposition affect the fate of N inputs to pot cultured beech seedlings?

Materials and methods

Site description

The experimental site is located in the mountain range Solling, Lower Saxony, Germany. The range is situated about 70 km southwards of Hannover. Solling (51°47′N and 9°37′E) with 740 km^2 area is elevated at 200–500 m a.s.l. and constitutes a watershed between rivers Weser and Leine. Geologically Solling is a uniform massive built of tertiary sandstone covered by a layer of loess at a thickness varying from 20 cm to 2 m (average 80 cm). In the Solling area Dystric Cambisols and Cambic Podsols dominate (FAO). Pseudogleys and stagnogleys also occur locally. Texture of soils is usually silty loam. The prevailing humus form is typical moder. Sixty percent of the surface of Solling is covered by forest. Pure spruce (*Picea abies* L. Karst.) stands constitute 31% of the forests, pure beech (*Fagus sylvatica* L.) stands 17% and mixed beech-spruce stands 24% (NMELF, 1996). The climate is characterized by a mean annual temperature of 6.5°C, mean annual precipitation of 1 050 mm and a frost-free period of 250 days. Three adjacent plots (area of each about 400 m^2) were chosen for the present study. They included a 100 to 120 year old stands of Norway spruce partly covered by grass, beech and a mixed spruce-beech stand.

Soil sampling and experimental design

In August of the first growing season some 120 intact soil columns (including forest floor) with 6.45 cm average depth were taken randomly from each stand (n = 40) using PVC cylinders (pots) with 15.2 cm (diameter) × 19 cm (depth). All soil samples were transferred to a green house partitioned into 4 wagons (250 cm length, 92 cm across, 26 cm height) with 10 replicates from soil samples of each stand at each one. The leachate from each sample passed through 10-cm quartz sand in a PVC cylinder set at the bottom of each pot, conducted the leachates through a silicon tube to a brown glass bottle. A cooling system was installed for circulating cool liquid permanently through a flexible tube spiraled four times around each pot to hold the temperature of the samples constant. The sides and the bottom of each wagon were isolated with a 4-cm thick Styropor. The empty spaces between the pots at each wagon filled with insulator materials to avoid the losses of temperature. The air and soil temperature were continuously recorded at 5 cm on top of the forest floor samples and at 3 cm depth (Fig. 1). The samples were artificially irrigated every two days using a bore hole PVC cap (5 cm height) contained small nylon threads which came through the fine holes. The pH and the applied amounts of cations, anions and heavy metals in throughfall were calculated on the basis of the long-term annual input at the study area (Matzner 1989). The element concentrations in the throughfall solution were constant during the experiment. The leachates volume of the soil solutions were collected in four weeks intervals and stored at 4°C until further processing.

Fig. 1 Experiment design and installations of pot cultured beech seedlings at the greenhouse

Treatments

Some 6–8 beech seeds were cultured in half of the pots (n = 60) in depth of 0.5 cm in the last week of August of first vegetation year, which germinated after about three weeks. The control treatments (including cultured and non-cultured), each with 18 replicates, received no nitrogen by throughfall. In the 15N tracer treatments (n = 84), cultured and non-cultured samples were supplied either with 1.17 $mg \cdot L^{-1}$ NO_3-N as $NH_4{}^{15}NO_3$ (n = 42) or with 1.18 $mg \cdot L^{-1}$ NH_4-N as $^{15}NH_4NO_3$ in throughfall (n = 42) for 442 days. The throughfall N input was in magnitude at the same rate of throughfall N input at Solling forest amounted to 1.59 $kg \cdot ha^{-1} \cdot a^{-1}$. The total throughfall volume added up to 816 mm and the amount of nitrogen input in fertilized cultured and non-cultured treatments over the course of experiment accounted for 1.92 $g \cdot m^{-2}$.

Seedlings biomass sampling and analyzes

Seed leaves and leaf samples of the first vegetation year were taken from the shoot tips about 15 weeks after bud break at December. Leaf samples of the second vegetation year were collected at mid November. Plant compartments were divided into seed leaves, leaf litter of the first and second growing seasons, stem, coarse roots (≥ 3 mm diameter) and fine roots (<3 mm diameter) which involved those in the forest soil containing mycorrhizal and non mycorrhizal root tips and fine roots developed in sand layer underneath. The root system partitioned by size and depth in order to represent some trends in biomass and ^{15}N distribution between the belowground biomass compartments. Roots were separated carefully from the forest soil (including forest floor) by washing and sieving method for several times.

All seedlings biomass compartments as well as the collected foliage litter (O_L) were dried at 65°C for 96 h, milled, homogenized and weighed before N content and ^{15}N analyzes. Stems and coarse roots were milled in a planetary mill, the other plant components ground in a piston-action ball mill.

^{15}N mass measurements

The $^{14}N/^{15}N$ isotope measurements were made with an isotope ratio mass spectrometer (Delta Plus, Finnigan Mat GmbH, Bremen, Germany) coupled to an elemental analyzer (EA 1108, Fisons, Rodano, Milan, Italy) in online mode. ^{15}N abundance is expressed in atom percent by the ratio:

$$\text{Atom \% } ^{15}\text{N} = \frac{^{15}N}{^{14}N+^{15}N}\times 100$$

Values of ^{15}N enrichment (atom % ^{15}N excess) were calculated by subtracting ^{15}N values from ^{15}N natural abundance of the control. For determination of ^{15}N concentrations of soil and plant materials, total N content and the biomass of the respective parts were taken into consideration.

Total ^{15}N content = $(^{15}Nt - {}^{15}Nc) \times [N] \times$ plant biomass or forest floor mass

Where $^{15}N_t$ and $^{15}N_c$ are the atom % concentrations of ^{15}N in treated and control plants, respectively, [N] is the total N concentration (of a g dry weight) of plant compartment. For estimation of ^{15}N uptake per plant, the ^{15}N concentrations of above- and belowground parts were summed up. Tracers recovered in pools were expressed as proportions of total ^{15}N tracer applied over the course of experiment.

$$\%^{15}\text{N}_{\text{recovery}} = \frac{[N_{pool}\times(atom\%^{15}N_{pool} - atom\%^{15}N_{control})\times m_{pool}]}{[N_{applied}\times(atom\%^{15}N_{tracer} - atom\%^{15}N_{ref.})]\times irrigationvolume}\times 100$$

Where $^{15}N_{\text{recovery}}$ is the percent ^{15}N tracer recovered in the labeled N pool (%), N_{pool} is the concentration of total N in the labeled N pool ($mg \cdot l^{-1}$), atom $\%^{15}N_{\text{pool}}$ is atom percent ^{15}N in the labeled N pool, atom $\%^{15}N_{\text{control}}$ is atom percent ^{15}N in the control (non-labeled) N pool, m_{pool} is N mass of the labeled N pool (g), N_{applied} is concentration of the fraction (NO_3-N or NH_4-N) in irrigated water ($mg \cdot l^{-1}$), atom $\%^{15}N_{\text{tracer}}$ is atom percent of the applied tracer, atom $\%^{15}N_{\text{ref.}}$ is atom percent ^{15}N in the reference (non-labeled) N pool and irrigation volume is total throughfall (l).

Gas measurements

Nitrous oxide fluxes from each soil sample were measured once per month from early October of the first growing season through late November of the second vegetation year. After closing the headspace by a gas-tight lid above the column, gas samples were taken with evacuated glass bottles (100 ml) after 0 and 20 min of incubation via small silicon tube connecting the lid and the glass bottle. Gas samples were analyzed by injection of gas sample into the port of a gas chromatograph (GC 14 A, Shimadzu, Duisburg, Germany) equipped with two detectors, a flame ionization detector (FID), and an electron capture detector (ECD) (Loftfield et al. 1997). The N_2O emissions were calculated using linear regression of the change in gas concentrations, based on the following equation:

$$F = k_{\text{N20}} \times \frac{273}{T} \times \frac{P}{101} \times \frac{V}{A} \times \frac{\Delta C}{\Delta t}$$

where F is the flux rate of N_2O ($\mu g \cdot m^{-2} \cdot h^{-1}$), k_{N2O} (1.25 $\mu g \cdot \mu l^{-1}$) is unit conversion factor for calculating N_2O flux rate, T is the air temperature (°K), P is the atmospheric pressure (kPa), V is the air volume of the headspace gas above the samples (l), A is the area of forest floor samples (m^2) and $\Delta C/\Delta t$ is the rate of change in concentration of N_2O, within the headspace ($\mu l \cdot l^{-1} \cdot h^{-1}$).

Soil biochemical analyzes

All forest soil samples of the control and ^{15}N-fertilized treatments were homogenized well to analyze nitrate and ammonium concentrations with 0.5M K_2SO_4 solution. Moisture content was determined on sub-samples by drying to constant weight at 105°C. Microbial C (C_{mic}) and N (N_{mic}) were determined using the chloroform fumigation-extraction method (Brookes et al. 1985). In total, 50 g field-moist sub-samples in two replicates were taken, One pair was immediately extracted with 0.5 M K_2SO_4 (approx. 5:1 ratio of solution to dry weight soil). The other pair was fumigated for 5 days with ethanol-free chloroform. Subsequently the chloroform was removed by evacuation and the soils were extracted by 0.5 M K_2SO_4 (~ 5:1 ratio of solution to dry mass soil). The differences in organic C and total N extracted between the fumigated and non fumigated samples (C and N flushes) are assumed to represent the C and N released from lysed soil microbes. The C and N flushes were converted to microbial biomass C and N, respectively, using a correction factor k_C = 0.45 (Joergensen 1996) and k_N = 0.68 for five day fumigated soils (Brookes et al. 1985). The Organic C in the K_2SO_4 extracts was analyzed by dry combustion at 680°C using TOC 5050 A shimadzu carbon analyzer (Shimadzu GmbH, Duisburg, Germany). The extracted ammonium, nitrate and total N were analyzed by a continuous flow system spectrophotometer (Skalar Analytic GmbH, 41812 Erkelenz, Germany). A sub-sample of forest soil (including forest floor) in each pot was analyzed to determine total C and N by dry combustion in a CN-auto analyzer (Vario, Elementar Analysensysteme, Hanau, Germany) and soil pH (digital pH-meter, WTW GmbH Wesl-Germany). One sub-sample in two replicates from control and ^{15}N-labeled forest soils were taken to analyze the values of ^{15}N in each soil sample by an isotope ratio mass spectrometer (Delta Plus, Finnigan Mat GmbH, Bremen, Germany).

Leachate chemical analyzes

Leachates were analyzed for NO_3^--N and NH_4^+-N and total N using a continuous flow system spectrophotometer (Skalar Analytic GmbH, 41812 Erkelenz, Germany). For estimation of ^{15}N in leachates, total dissolved nitrogen (TDN) in ^{15}N fertilized and reference samples were determined using an adaptation of the persulfate-base digestion procedure technique in which all NO_3^- present is volatilized as HNO_3 in closed tubes prior to ^{15}N diffusion (Wyland et al. 1994; Stark and Hart 1996). The ^{15}N enrichment was measured by the continuous flow system spectrophotometer after oxidation of 10 ml of percolate in 10 ml oxidizing reagent followed by steam distillation of the percolate with 10 M NaOH to buffer the solution and volatilize NH_3 and evaporation of the $(NH_4)_2SO_4$ distillates adjusted to pH 4. This method is preferred over the Total Kjeldahl Nitrogen method for samples containing high amounts of NO_3^-, since NH_4^+ and organic nitrogen are converted to NO_3^-.

Statistical analyses

The Mann-Whitney U-Test at $p<0.05$ level, was used to evaluate the significance of differences between the treatments in individual plant compartments, performed by the program Statistica version 6.0.

Results and discussion

N budgets

Estimated nitrogen budgets for all treatments were calculated as a total input minus output (leaching and N_2O fluxes) and net plant N uptake over the incubation period (Table 1). Total input of nitrogen applied as ^{15}N-labeled NH_4NO_3 was equivalent 1.92 $g \cdot m^{-2}$. In cultured treatments nitrogen leaching losses varied between 6.41 $g \cdot m^{-2}$ and 7.58–10.0 $g \cdot m^{-2}$ at control and ^{15}N-fertilized treatments. In corresponding non-cultured treatments the values of the leached N ranged from 8.02 $g \cdot m^{-2}$ to 11.6–9.58 $g \cdot m^{-2}$. The amounts of nitrogen leaching losses increased markedly with N additions across the control and ^{15}N-fertilized treatments. The balance values of N_2O-N efflux between the cultured treatments ranged from 0.42 $g \cdot m^{-2}$ at control to 0.54–0.40 $g \cdot m^{-2}$ at ^{15}N-fertilized and varied between 0.46 $g \cdot m^{-2}$ and 0.52–0.41 $g \cdot m^{-2}$ in corresponding non-cultured treatments. Analyses of variance ($p < 0.05$) revealed no significant effect of ^{15}N-fertilizer on balanced values of N_2O-N losses between the cultured and non-cultured treatments. The N_2O-N flux rates observed in our study were in magnitude in consistent with the flux rates at Solling forest, Germany, subjected to high levels of atmospheric N deposition (Brumme and Beese 1992; Brumme et al. 1999). The net nitrogen uptake by beech seedlings from forest soil supply in control (1.36 $g \cdot m^{-2}$) and ^{15}N-fertilized treatments (1.01–1.66 $g \cdot m^{-2}$) were not significantly affected with N additions. The calculated balance values of nitrogen (N budgets) over the incubation period ranged from -8.19 $g \cdot m^{-2}$ in control to -9.62–-8.14 $g \cdot m^{-2}$ in ^{15}N-fertilized cultured treatments and varied between -8.48 $g \cdot m^{-2}$ and -10.1–-8.07 $g \cdot m^{-2}$ in corresponding non-cultured treatments. Comparing the balance values of nitrogen across the treatments showed a tendency to increase on net nitrogen mineralization after ^{15}N-nitrate application; although no significant effect of N additions were detected between the control and ^{15}N-fertilized treatments. Aber et al. (1989) hypothesized a slow, continuous increase in net N mineralization as added nitrogen was incorporated into the cycle through plant uptake, litter fall, and decomposition. In consistent, Gunderson et al. (1998) reported increases in field measured net N mineralization rates with N additions only at N limited sites, while those with high initial rates of N cycling showed decreases in net N mineralization with further N additions. Aber et al. (1998) reported initial increases in N mineralization with chronic N additions at the Harvard Forest study site were followed by actual decreases in net N mineralization by the sixth year of application. The ΔN balance difference between the cultured and non-cultured treatments were after ^{15}N-NO_3^- (0.48 $g \cdot m^{-2}$) slightly higher and after ^{15}N-NH_4^+ (-0.07 $g \cdot m^{-2}$) lower than the ΔN balance difference of the control cultured and non-cultured treatments (0.28 $g \cdot m^{-2}$). These data implies nearly equal total N balance across the treatments, as the biomass and N concentration of the fine roots in ^{15}N-fertilized were not affected with N additions compared to control cultured treatments.

Microbial immobilization of Nitrogen affected by N input

The effect of N tracer input on microbial immobilization through measurements of microbial biomass (C_{mic}) in forest soil (including forest floor) differed between the treatments. While the values of microbial biomass C in ^{15}N-fertilized plant treatments were markedly higher than the values of corresponding control plant treatment, no significant effect of N additions were detected between the non-cultured treatments (Table 2). The same trend of differences was detected also by comparing the microbial C/N ratios between the ^{15}N-fertilized cultured and non-cultured with corresponding control treatments. Analyses of variance ($p<0.05$) revealed no significant differences on N immobilization by microbial biomass (N_{mic}) across the control and the corresponding cultured and non-cultured ^{15}N-fertilized treatments. This can be explained partly by rapid microbial immobilization/ re-mineralization of added mineral N as the major process by which added nitrate and ammonium immobilized in the forest soil. At the present study, after 442 days of tracer application the amounts of ^{15}N retained in the forest soils accounted for 32.2–31.4 mg m^{-2} after ^{15}N-ammonium versus 12.0–8.29 $mg \cdot m^{-2}$ after ^{15}N-nitrate in cultured and non-cultured treatments (Table 5). The total recoveries of the applied ^{15}N retained in the forest soils of cultured and non-cultured samples accounted for 34.6%–33.7% after ^{15}N-NH_4^+ versus 13.1%–9.0% after ^{15}N-NO_3^- in fertilized cultured and non-cultured treatments. This states that biotic and abiotic ammonium assimilation capacities of forest soils were more exceeded with N additions, than were the nitrate assimilation capacities (Durka et al. 1994; Buchmann et al. 1996), as tracer recoveries from forest soils (including for-

est floor) were three times greater when ^{15}N-NH_4^+ rather than ^{15}N-NO_3^- were applied. Short term studies of ^{15}N immobilization into forest soils reveal that a significant portion of labeled N is incorporated into non-extractable or recalcitrant pools (e.g., Vitousek and Matson 1985). Groffman et al (1993) traced ammonium and nitrate in a temperate forest in Michigan, USA, and found higher immobilization rates for ammonium (60%) than for nitrate (48%) in a short term experiment in forest soils. Nadelhoffer et al. (1992) reported similar results for a ^{15}N-ammonium tracer study in a hardwood mixed forest where 67% of the ^{15}N input was found in the surface soil (0–5 cm) after one growing season. Strickland et al. (1992) demonstrated rapid incorporation of ^{15}N into a non-microbial, physically shielded soil pool (slow turnover pool) but stated that the mechanisms by which the process accomplished need further study. Most of the ^{15}N pool dilution studies show a near immediate disappearance of labeled N, which has been attributed to abiotic processes (e.g. Schimel and Firestone 1989). These results are consistent with the model of Aber et al. (1991) who modeled the fate of N under "nitrogen saturation" conditions and predicted that a large percentage of nitrogen would be held in the soil organic matter.

Table 1. The input and leachate of nitrogen, total plant N uptake, the balance values of N_2O emissions and the total balance of nitrogen within the control (*n*=18) and the two labelled-N forms (*n*=21) of the ^{15}N-fertilized plants and non-plants treatments over the experiment.

treatment	N-input ($g \cdot m^{-2}$)	N-leachate ($g \cdot m^{-2}$)	N_2O-N efflux ($g \cdot m^{-2}$)	plant N uptake ($g \cdot m^{-2}$)	N balance	Δ N balance
control (plants)	0	6.41 (0.58)	0.42 (0.33)	1.36 (1.96)	-8.19 (2.07)	0.28
control	0	8.02 (0.83)	0.46 (0.64)	–	-8.48 (1.05)	
$NH_4{}^{15}NO_3$ (plants)	1.92 (0.009)	10.0 (1.24)	0.54 (0.42)	1.01 (1.90)	-9.62 (2.31)	0.48
$NH_4{}^{15}NO_3$	1.92 (0.009)	11.6 (1.08)	0.52 (0.54)	–	-10.1 (1.20)	
$^{15}NH_4NO_3$ (plants)	1.92 (0.016)	7.58 (0.82)	0.40 (0.28)	1.66 (1.93)	-8.14 (2.11)	-0.07
$^{15}NH_4NO_3$	1.92 (0.016)	9.58 (0.93)	0.41 (0.24)	–	-8.07 (0.96)	

Notes: Standard deviation is given in parentheses.

Table 2. Mean characteristics of forest soil (including forest floor) at the control (*n*=18) and ^{15}N-fertlized plants and non-plants treatments (*n*=21), measured at the end of the experiment

treatment	depth	mass	pH		C_{org}	N_{tot}	C/N	C_{mic}	N_{mic}	C_{mic}/N_{mic}	C_{mic}/C_{org}
	(cm)	($Mg \cdot ha^{-1}$)	(H_2O)	(KCl)	($g \cdot kg^{-1}$)			($mg \cdot kg^{-1}$)			
control (plants)	6.67	242	3.69	2.98	172	8.83	19.2	1768	158.0	11.50	1.05
	(0.83)	(76.0)	(0.34)	(0.43)	(60.8)	(2.71)	(1.63)	(583)	(57.0)	(1.86)	(0.17)
control	6.72	227	3.74	2.92	170	9.94	18.2	1924	159.5	12.40	1.19
	(1.00)	(66.4)	(0.34)	(0.39)	(78.6)	(4.58)	(3.22)	(826)	(77.8)	(2.07)	(0.27)
$NH_4{}^{15}NO_3$ (plants)	6.33	205	3.68	2.98	175	8.94	19.4	2266	187.4	12.10	1.32
	(0.90)	(67.4)	(0.33)	(0.31)	(62.3)	(2.80)	(1.27)	(722)	(58.3)	(1.16)	(0.24)
$NH_4{}^{15}NO_3$	6.17	222	3.71	(2.92)	144	7.92	18.0	1732	150.2	11.60	1.22
	(1.20)	(52.5)	(0.32)	(0.33)	(36.8)	(1.62)	(1.47)	(473)	(43.2)	(1.18)	(0.28)
$^{15}NH_4NO_3$ (plants)	6.38	256	3.74	3.06	142	7.13	20.9	1973	161.7	12.40	1.30
	(1.42)	(74.6)	(0.43)	(0.46)	(49.7)	(2.03)	(2.16)	(710)	(65.3)	(1.11)	(0.39)
$^{15}NH_4NO_3$	6.45	239	3.71	2.92	147	7.93	18.3	2002	159.3	12.70	1.43
	(1.53)	(73.6)	(0.46)	(0.47)	(51.4)	(2.20)	(2.18)	(665)	(55.5)	(1.40)	(0.53)

Notes: Standard deviation is given in parentheses.

^{15}N tracer partitioning in plants

The partitioning of both ^{15}N tracers in the beech seedlings followed the same pattern of total N distribution. Among the aboveground compartments stems with 39% of the seedlings total biomass comprised 0.035–0.041 $mg \cdot g^{-1}$ of ^{15}N tracer retained (Table 3) and (Table 4). The larger amounts of ^{15}N retained in stems may be attributed to direct uptake or absorption from throughfall solution. In addition, nitrogen uptake by the foliage and re-translocation during the senescence period can also be involved. Comparing the values of ^{15}N tracer retained between the leaf litter of the first (0.006–0.007 $mg \cdot g^{-1}$) and second growing seasons (0.013–0.015 $mg \cdot g^{-1}$) revealed that the perennial species at first growing season rely partly on tissue reserves for their N nutrition. The least values of ^{15}N tracer retained in the aboveground compartments were observed in buds (0.031–0.037 $mg \cdot g^{-1}$) and seed leaves (0.006 $mg \cdot g^{-1}$), where they contribute to 6.29% and 6.85% of total seedlings biomass, respectively. Comparing the below ground compartments coarse roots due to a larger pool size (20.5% of the total seedling biomass production) comprised 0.050–0.065 $mg \cdot g^{-1}$ of ^{15}N tracer retention (Table 3) and (Table 4). The retained ^{15}N in roots can be attributed to direct N uptake and to some extent foliage litter re-translocation of nitrogen products at the end of the season. The fine roots system grew in forest soil and sand layer underneath accounted for 0.034–0.037 $mg \cdot g^{-1}$ and 0.096–0.130 $mg \cdot g^{-1}$ of ^{15}N tracer uptake, although they comprised only 4.77%–5.73% of the total plant biomass. In consistent with Nadelhoffer et al. (2002) the differences between total fine root biomass in fertilized and non-fertilized treatments (10.5

vs.10.7%) were not statistically significant, suggesting that fine root turnover and production either, do not vary or that they tend to decrease as N availability increases. In consistent with Magill et al. (1997), the concentration of the ^{15}N tracer retained in the fine roots system can account for a substantial fraction of N immobilization in the plants. Immobilization of deposited ^{15}N labeled nitrogen by mycorrhizal fine roots may increase the ^{15}N sequestration by their turnover which may be detectable in the soil organic matter. A higher ^{15}N incorporation in the forest floor with beech seedlings indicated that plants may have improved the N immobilization. The total amount of ^{15}N tracer retained in seedlings were lower after ^{15}N-NH_4^+ than after ^{15}N-NO_3, suggesting that nitrate uptake and deposition could have a greater proportion on seedlings growth than ammonium uptake and deposition. Nitrate may be assimilated by the plants by high energy costs involved in nitrate reduction in fine roots, or can utilize extra reductant from the light reactions of photosynthesis to reduce nitrate in foliage (Nadelhoffer et al. 1984).

Table 3. Total biomass content per seedling (mg) and percentage of the biomass of seeds, above- and belowground compartments to total seedlings biomass at the end of experiment in control and ^{15}N-fertilized treatments

pool	plant biomass			
	control		^{15}N-fertilized	
	(mg)	(%)	(mg)	(%)
seeds	357	28.6	357	30.7
seed leaves	74.4 (15.4)	5.96	79.7 (23.8)	6.85
buds	69.4 (26.0)	5.57	73.2 (39.2)	6.29
leaf litter (1st year)	89.1 (46.0)	7.14	106 (45.2)	9.13
leaf litter (2nd year)	139 (113)	11.1	157 (75.5)	13.5
stems	495 (172)	39.7	454 (23.6)	39.0
aboveground (total)	805 (265)	64.4	803 (310)	68.7
coarse roots	310 (116)	24.8	238 (112)	20.5
fine roots in forest soil	55.6 (36.1)	4.46	55.5 (27.5)	4.77
fine roots in sand layer	77.6 (38.4)	6.22	66.6 (45.5)	5.73
belowground (total)	443 (150)	35.6	360 (136)	31.3
plant (total)	1248 (385)	100	1163 (427)	100

Notes: Standard deviation is given in parentheses.

Recoveries were highest in stems, where the ^{15}N tracer recovery ranged from 6.92%–6.40% after ^{15}N- NH_4^+ versus ^{15}N-NO_3 additions. Coarse roots, total fine roots system and leaf litter of the second and first growing seasons exhibited lower values of N tracer recoveries, respectively. The least values for tracer recoveries in beech seedlings were detected in seed leaves, varied between 0.20%–0.16% after ^{15}N-NH_4^+ vs. ^{15}N-NO_3^-. The sum of tracers recovered in measured pools ranged from 17.1% to 19.0 % of ^{15}N additions, where total percent recoveries were higher after ^{15}N-NO_3^- than after ^{15}N-NH_4^+ inputs. The results of the percentage recoveries in different plant compartments suggests that the fertilized N taken up by seedlings are assimilated mainly into stems, coarse roots and total fine roots system. Although fluxes of tracers into seedlings biomass were small, the fact that ^{15}N recoveries in plant compartments were higher after ^{15}N-NO_3^- than after ^{15}N-NH_4^+ additions, suggests that nitrate deposition could have a greater effect on seedlings growth than ammonium deposition. Some tracer studies are consistent with our finding that trees compete better for nitrate than for ammonium inputs. For instance, Nadelhoffer et al. (1999) found total percent recoveries of ^{15}N in the oak and red pine plantations were typically greater after ^{15}N-NO_3^- than after ^{15}N-NH_4^+ additions. Studies of cation surplus in beech tree leaves in relation to assimilated nitrogen (Beese 1986) indicated that the beech trees take up mineral nitrogen primarily in the form of nitrate which is then reduced in the leaves. The processes which could have contributed to greater recoveries of tracer after ^{15}N-NO_3^- than after ^{15}N-NH_4^+ additions may be the tree species preference for nitrate, or greater competition between tree roots and soil microbes for ammonium (microbial preference for ammonium) , or more rapid movement of nitrate to root surfaces (Nadelhoffer et al. 1999). Any or all of these processes could have to some extent contributed to greater recoveries of tracer after ^{15}N-NO_3^- than after ^{15}N-NH_4^+ inputs. Comparing percent recoveries of ^{15}N in above- and belowground compartments revealed that most of the ^{15}N taken up by the plants was used to build up the above ground seedlings (53.9%–46.8%), while coarse roots and total fine roots system accounted for (28.1%–30.3%) and (18.1%–22.8%) after ^{15}N-NH_4^+ and ^{15}N-NO_3^-, respectively.

Table 4. The concentration ($mg \cdot g^{-1}$) and amount ($mg \cdot m^{-2}$) of ^{15}N tracer retained and the percentage tracer recoveries of applied ^{15}N in above- and below-ground compartments of the beech seedlings and in the whole plant (n = 42).

pool	^{15}N tracer retained				^{15}N tracer recovered (%)	
	^{15}N-NH_4^+		^{15}N-NO_3^-		^{15}N-NH_4^+	^{15}N-NO_3^-
	($mg \cdot g^{-1}$)	($mg \cdot m^{-2}$)	($mg \cdot g^{-1}$)	($mg \cdot m^{-2}$)		
buds	0.031 (0.01)	0.84 (0.32)	0.037 (0.01)	1.22 (0.49)	0.90	1.32
seed leaves	0.006 (0.00)	0.19	0.006 (0.00)	0.15	0.20	0.16
leaf litter (1st year)	0.006 (0.00)	0.22 (0.10)	0.007 (0.00)	0.24 (0.09)	0.23	0.26
leaf litter (2nd year)	0.015(0.00)	0.90 (0.48)	0.013 (0.00)	0.69 (0.31)	0.97	0.75
stems	0.035 (0.01)	6.44 (3.45)	0.041 (0.02)	5.90 (3.38)	6.92	6.40
coarse roots	0.050 (0.01)	4.46 (1.84)	0.065 (0.02)	5.29 (2.95)	4.80	5.75
forest floor fine roots	0.034 (0.02)	0.63 (0.34)	0.037 (0.03)	0.70 (0.61)	0.68	0.76
fine roots in sand layer	0.096 (0.03)	2.25 (1.30)	0.130 (0.03)	3.28 (2.64)	2.42	3.57
plant (total)	0.034 (0.03)	15.9 (4.18)	0.042 (0.04)	17.5 (5.28)	17.1	19.0

Notes: Standard deviation is given in parentheses.

^{15}N tracer partitioning in total plant-soil system

The retention of the^{15}N tracer in each component of total system will reflect the partitioning of ammonium-N and nitrate-N input entering the forest soil. It was detected that the proportion of labeled N in seedlings after two successive growing seasons in tendency was higher after ^{15}N-NO_3^- than after ^{15}N-NH_4^+ (Table 5). Percentage recoveries of the applied ^{15}N within the plants$_{(total)}$ were also higher after ^{15}N-NO_3^- application than after ^{15}N-NH_4^+ additions, suggests that nitrate-N additions could have a greater effect on seedlings growth than ammonium-N, although no significant differences were detected with respect to NH_4^+ and NO_3^- incorporation in plants. The average tracer recoveries of the applied ^{15}N across both N forms in beech seedlings (18.0%) revealed lower importance of seedlings as sinks for N inputs as compared to forest soil (23.8%–21.4%). In consistent with Nadelhoffer et al.(1993, 1995, 1999), forest soil in our study appeared to be stronger sinks for ^{15}N additions than were plants. Comparing the retention values between the plants and forest soils in the present study indicated that the ^{15}N-NH_4^+ in forest soil retained two times higher than in the plants, while the ^{15}N-nitrate retention in forest soil was slightly lower than that of the plants. The concentration of the ^{15}N tracers retained in O_F/O_H plus mineral soil after ^{15}N-NH_4^+ and ^{15}N-NO_3^- were lower than the corresponding values in O_L, however due to much higher mass the sink strength in O_F/O_H plus mineral soil were significantly higher than the corresponding values in O_L in the cultured and non-cultured treatments (Table 5). Tracer recoveries in forest soils were significantly influenced by the form of N label applied. The tracer recoveries of the applied ^{15}N retained into O_L accounted for 5.09%–8.36% after ^{15}N- NH_4^+ and 2.33%–2.62% after ^{15}N- NO_3^-, while the percentage recoveries of added ^{15}N assimilated into O_F/O_H plus mineral soil varied between 29.50%–25.40% after ^{15}N-NH_4^+ and 10.70%–6.38% after ^{15}N-NO_3^- in cultured and non-cultured treatments. In consistent with Groffman et al. (1993) and Buchmann et al. (1996) more ^{15}N-ammonium was incorporated into the forest soil (32.2–31.4 mg·m^{-2}) than ^{15}N-nitrate (12.0–8.29 mg·m^{-2}) in cultured and non-cultured treatments. This can be explained by the preference of ammonium to nitrate by soil microorganisms, followed by higher microbial immobilization of ammonium and also adsorption of ammonium through pure physicochemical reactions onto exchange sites of organic matter, while nitrate due to a lower retention capacity relative to ammonium is lost mainly into leachate (e.g. Matschonat and Matzner 1996; Aber et al. 1998). This could be seen after two growing seasons of ^{15}N tracer application that more ^{15}N-nitrate than ^{15}N-NH_4^+ were incorporated into leachate (Table 6).

Table 5. The concentration (mg/g) and the amount of ^{15}N tracer retained or leached (mg·m^{-2}) and the percentage of tracer recoveries in plant$_{(total)}$, O_L, O_F/O_H plus mineral soil, forest soil (including forest floor) and in leachate at ^{15}N-fertilized plants and non-plants treatments (n = 42).

Pool	^{15}N tracer retained or leached				^{15}N tracer recovered		Mean ^{15}N recovery
	^{15}N-NH_4^+		^{15}N-NO_3^-		^{15}N-NH_4^+	^{15}N-NO_3^-	
	(mg·g^{-1})	(mg·m^{-2})	(mg·g^{-1})	(mg·m^{-2})	%	%	
plant $_{(total)}$	0.034 (0.03)	15.9 (4.18)	0.042 (0.04)	17.5 (5.28)	17.1	19.0	18.03
O_L (plants)	0.022 (0.01)	4.74 (2.35)	0.010 (0.01)	2.14 (0.89)	5.09	2.33	3.71
O_F/O_H +mineral soil(plants)	1.20×10^{-3}	27.5 (12.8)	0.50×10^{-3}	9.88 (6.89)	29.5	10.7	20.1
forest soil (plants)		32.2 (13.0)		12.0 (6.95)	34.6	13.1	23.8
leachate (plants)	0.041 (0.02)	21.6 (2.71)	0.079 (0.03)	49.1 (5.42)	23.2	53.3	38.3
O_L	0.034 (0.02)	7.78 (6.66)	0.013 (0.01)	2.41 (1.45)	8.36	2.62	5.49
O_F/O_H +mineral soil	1.03×10^{-3}	23.6 (5.54)	0.28×10^{-3}	5.88 (2.30)	25.4	6.38	15.9
forest soil		31.4 (8.66)		8.29 (2.72)	33.7	9.00	21.4
leachate	0.051(0.01)	31.3 (3.21)	0.098 (0.02)	72.8 (5.57)	33.6	79.1	56.3

Notes: Standard deviation is given in parentheses.

Table 6. ^{15}N tracer input, output and retention efficiencies, the amounts of tracer retained in plant, forest soil (including forest floor), and the balance values of ^{15}N excess (mg·m^{-2}) and the percentage of the tracer lost in the ^{15}N-fertilized plants (n = 21) and non-plants (n = 21) treatments.

treatment	^{15}N-input (mg·m^{-2})	^{15}N-output (mg·m^{-2})	^{15}N retention efficiency(%)	^{15}N tracer retained (mg·m^{-2}) plant$_{(total)}$	forest soil	^{15}N balance	^{15}N lost (%)
$NH_4{}^{15}NO_3$ (plants)	92.1 (0.68)	49.1 (5.42)	46.7	17.5 (5.28)	12.0 (6.95)	13.5 (10.3)	14.7
$NH_4{}^{15}NO_3$	92.1 (0.68)	72.8 (5.57)	21.0	–	8.29 (2.72)	11.0 (6.23)	11.9
$^{15}NH_4NO_3$ (plants)	93.1 (1.24)	21.6 (2.71)	76.8	15.9 (4.18)	32.2 (13.0)	23.3 (14.0)	25.1
$^{15}NH_4NO_3$	93.1 (1.24)	31.3 (3.21)	66.4	–	31.4 (8.66)	30.4 (9.32)	32.7

Notes: Standard deviation is given in parentheses.

The results of ^{15}N retention efficiencies after ^{15}N-NO_3^- and ^{15}N-NH_4^+ in cultured and non-cultured treatments represented

lower retention capacity of nitrate relative to ammonium, resulted in higher fluxes of ^{15}N-NO_3^- from forest floor into leachate. The observed movement of ^{15}N tracer through the forest floor demonstrated that although the forest soil due to high immobilization capacity were the important sink for nitrogen, however leaching losses of the applied tracer represented a significant proportion of the total N input. In consistent, Durka et al. (1994) indicated that the movement of ^{15}N tracer through the forest floor corresponds well with estimates of the leaching rates of deposited nitrate.

^{15}N tracer budget

Estimating the balance values of $^{15}N_{(excess)}$, as the difference between ^{15}N input and the amounts of the tracer in leachate and the ^{15}N retained in $plants_{(total)}$ and forest soil (including forest floor), indicated higher ammonium retention capacity than nitrate in the system as a result of nitrification and the requirement to maintain a constant N concentration in equilibrium between N-immobilization and mineralization. Total recovery rates of the applied ^{15}N in the whole system accounted for 85.3%–88.1% after ^{15}N-NO_3^- and 67.3%–74.9% after ^{15}N- NH_4^+ in cultured and non-cultured treatments, respectively. The labeled ^{15}N not recovered in the investigated parts amounted to 14.7%–11.9% after ^{15}N-NO_3^- and 25.1%–32.7% after ^{15}N-NH_4^+ in cultured and non-cultured treatments, has presumably been lost by denitrification (Table 6). In agreement with our results Mochoge and Beese (1983) demonstrated losses of labeled nitrogen in forest soils in the range of 10%–35%. Melin et al. (1983) reported the rates of the labeled N lost after two successive growing seasons NH_4NO_3 fertilizer application in a *Pinus sylvestris* stand amounted to 11%–31%. Our data further exhibited that the losses after ^{15}N-NH_4^+ addition were up to 2.7 times higher than after ^{15}N-NO_3^- application. This may presumably due to the transport behavior of these ions in the forest floor. The anionic nitrate which did not interact with the organic matter was leached out much faster than the cationic ammonium. Consequently, there was not enough time for further nitrate transformations as was the case for ammonium. The ^{15}N retention efficiency (percentage of added ^{15}N retained) over the experiment period was 46.7%–21.0% after ^{15}N-NO_3^- and 76.8%–66.4% after ^{15}N- NH_4^+ in cultured and non-cultured treatments, respectively, exhibiting the effect of plants especially the role of mycorrhizal fine roots in sequestration of added ^{15}N which has been resulted in improved retention capacity of nitrogen in cultured treatments.

Conclusion

The results of the present study demonstrated that the applied nitrogen in plant available forms to a lower extent is taken up directly by the plants leading to an immobilization via the litter and forest soil. In this ^{15}N tracer study, the organic soil horizon was identified as the major N sink for ammonium and nitrate deposition, reflecting a high immobilization capacity of soil microorganisms. The percentage recoveries of ^{15}N retained in the forest soil (including forest floor) were about three times higher when ^{15}N-NH_4^+ was applied compared to ^{15}N-NO_3^-. Because ^{15}N-NH_4^+ and ^{15}N-NO_3^- in equivalent amounts were applied the presented results can be used to determine how forms and rates of the N-input affects the distribution of nitrogen into different components of the system. The form of N input influenced its movement into plant pools. It was demonstrated that beech seedlings assimilate nitrogen mainly in the form of nitrate, which is then reduced in the leaves, although the differences between the retention of NO_3^--N and NH_4^+-N in plants were not statistically significant. It was evident that not the plants but the microorganisms can responsible for a substantially higher retention of NH_4^+ than NO_3^- in total plant-soil system.

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References

Aber JD, McDowell WH, Nadelhoffer KJ, Magill A, Berntson G, Kamakea M, McNulty SG, Currie W, Rustad L, Fernandez I. 1998. Nitrogen saturation in temperate forest ecosystems. Hypotheses revisited. *Bio Science*, **48**: 921–934.

Aber JD, Magill AH, Boone R, Melillo JM, Steudler P, Bowden R. 1993. Plant and soil responses to chronic nitrogen additions at the Harvard Forest, Massachusetts. *Ecological Applications*, **3**: 156–166.

Aber JD, Nadelhoffer KJ, Steudler P, Melillo JM. 1989. Nitrogen saturation in northern forest ecosystems. *Bio Science*, **39**: 378–386.

Aber JD.1992. Nitrogen cycling and nitrogen saturation in temperate forest ecosystems. *Trend Ecol Evolut*, **7**: 220–223.

Aber JD, Melillo JM, Nadelhoffer KJ, Pastor J, Boone RD. 1991. Factors controlling nitrogen cycling and nitrogen saturation in northern temperate forest ecosystems. *Ecological Applications*, **1**: 303–315.

Beese F. 1986. Parameter des Stickstoffumsatzes in Ökosystemen mit Böden unterschiedlicher Acidität. *Göttinger Bodenk Ber,* **90**: 344.

Bowden RD, Melillo JM, Steudler PA, Aber JD. 1991. Effects of nitrogen additions on annual nitrous oxide fluxes from temperate forest soils in the North eastern United States. *J Geophys Res,* **96** (D5): 9321–9328.

Brumme R, Borken W, Finke S. 1999. Hierarchical control on N_2O emissions in forest ecosystems. *Global Biogeochemical Cycles,* **13(**4): 1137–1148.

Brookes PC, Landman A, Pruden G, Jenkinson DS. 1985. Chloroform fumigation and the release of soil nitrogen. *Soil Biol and Biochem*, **17**: 837–842.

Brumme R, and Beese F. 1992. Effects of liming and nitrogen fertilization on emissions of CO_2 and N_2O from a temperate forest. *J Geophys Res*, **97**: 12851–12858.

Buchmann N, Gebauer G, Schulze ED. 1996. Partitioning of ^{15}N-labeled ammonium and nitrate among soil, litter, below- and above-ground biomass of trees and understory in a 15-year-old Picea abies plantation. *Biogeochemistry*, **33**: 1–23.

Davidson EA, Myrold DD, Groffman PM. 1990. Denitrification in temperate forest ecosystems. Pages 196-220. Sustained productivity of forest soils. Faculty of Forestry publications. University of British Colombia, Vancou-

ver, Canada.

Dise NB, Wright RF. 1995. Nitrogen leaching in European forests in relation to nitrogen deposition. *For Ecol and Manage,* **71**: 153–162.

Durka W, Schulze ED, Gebauer G, Voerkelius S. 1994. Effects of forest decline on uptake and leaching of deposited nitrate determined from ^{15}N and ^{18}O measurements. *Nature,* **372**: 765–767.

Galloway JN, Schlesinger WH, Levy II H, Michaels A, Schnoor JL. 1995. Nitrogen fixation: atmospheric enhancement-environmental response. *Global Biogeochemical Cycles,* **9**: 235–252.

Groffman PM, Zak DR, Christensen S, Mosier A, and Tiedje JM. 1993. Early spring nitrogen dynamics in a temperate forest landscape. *Ecology*, **74**: 1579–1585.

Gundersen P, Emmet BA, Kjonaas OJ, Koopmans CJ, Tietema A. 1998. Impact of nitrogen deposition on nitrogen cycling in forests: a synthesis of NITREX data. *For Ecol and Manage*, **101**: 37–56.

Joergensen RG. 1996. The fumigation-extraction method to estimate soil microbial biomass: *Soil Biol and Biochem*, **28**: 25–31.

Loftfield N, Flessa H., Augustin J, Beese F. 1997. Automated gas chromatographic system for rapid analysis of the atmospheric trace gases methane, carbon dioxide, and nitrous oxide. *J Environ Qual,* **26**(2): 560–564.

Magill AH, Aber JD, Hendricks JJ, Bowden RD, Melillo JM, Steudler PA. 1997. Biogeochemical Response of Forest Ecosystems to Simulated Chronic Nitrogen Deposition. *Ecological Applications*, **7**(2): 402–415.

Magill AH, Downs KJ, Nadelhoffer RA, Hallet RA, Aber JD. 1996. Forest ecosystem response to four years of chronic nitrate and Sulfate additions at Lead Mountain, Maine. *Forest Ecol and Manage*, **84**: 29–37.

Magill AH, Aber JD, Berntson GM, McDowell WH, Nadelhoffer KJ, Melillo JM, Steudler P. 2000. Long-term nitrogen additions and nitrogen saturation in two temperate forests. *Ecosystems*, **3**(3): 238–253.

Matschonat G, Matzner E. 1996. Soil chemical properties affecting NH_4^+ sorption in forest soils. *Z Pflanzenern u Bodenk*, **159**(5): 505–511.

Matzner E. 1989. Acid precipitation: case study Solling. Pages 95-115. New York, USA: Springer-Verlag,.

Melin J, Nommik H, Lohm U, Flower-Ellis J. 1983. Fertilizer nitrogen budget in Scots pine ecosystem attained by using root-isolated plots and ^{15}N tracer technique. *Plant and Soil,* **74**: 249–263.

Mochoge B, Beese F. 1983. The behavior of nitrogen fertilizers in natural and acid loess soils. II. Distribution and balance of ^{15}N-tagged nitrogen. *Z Pflanzenern u Bodenk,* **146**: 504–515.

Mulholland PJ, Tank JL, Sanzone DM, Wollheim WM, Peterson BJ, Webster JR, Meyer JL. 1999. Nitrogen Cycling in a Forest Stream Determined by a ^{15}N Tracer addition. *Ecological Monographs*, **70**(3): 471–493.

Nadelhoffer Kj, Aber JD, Melillo JM. 1984. Seasonal patterns of ammonium and nitrate uptake in nine temperate forest ecosystems. *Plant and Soil*, **80**: 321–335.

Nadelhoffer Kj, Downs MR, Fry B, Magill A, Aber JD. 1999. Controls on N retention and exports in a fertilized watershed. *Environ Monitoring and Assessment*, **55**(1): 187–210.

Nadelhoffer KJ, Downs MR, Fry B, Aber JD, Magill AH, Melillo JM. 1995. The fate of ^{15}N-labelled nitrate additions to a northern hardwood forest in eastern Maine, USA. *Oecologia*, **103**: 292–301.

Nadelhoffer KJ, Downs MR, Fry B. 1999. Sinks for ^{15}N-enriched additions to an oak forest and a red pine plantation. *Ecological Applications,* **9**: 72–86.

Nadelhoffer KJ, Aber JD, Downs MR, Fry B, Melillo JM. 1993. Biological sinks for nitrogen additions to a forested catchment. Experimental manipulations of biota and biogeochemical cycling in ecosystems: approach, methodologies, Findings (CEC Ecosystems Research Report no.(4)ECSC-EEC-EAEC. Brussels, Luxembourg. PP.64–70.

Nadelhoffer KJ, Aber JD, Downs MR, Fry B, Melillo JM. 1992. Biological sinks for N additions to a forested catchment. In: Rasmussen L, Bridges T and Mathy P (EDS) Proceedings " Experimental Manipulations of Biota and Biogeochemical Cycling in ecosystems", 18–20 May 1992 (pp 64 –70). Copenhagen, Denmark.

Nadelhoffer KJ, Emmett BA, Gundersen P, Kjonaas OJ, Koopmans CJ, Schleppi P, Titema A, Wright RF. 1999. Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests. *Nature*, **398**: 145–148.

Nadelhoffer KJ, Johnson L, Laundre J, Giblin AE, Shaver GR. 2002. Fine root production and nutrient content in wet and moist arctic tundras as influenced by chronic fertilization. *Plant and Soil,* **242**(1): 107–113.

NMELF (Nieedersächsisches Ministerium für Ernährung, Landwirtschaft und Forsten). 1996:Waldentwicklung Solling. Fachgutachten. P. 14–15.

Preston CM, Marshall VG, McCullough K, Mead DJ. 1990. Fate of ^{15}N-labelled fertilizer applied on snow at two forest sites in British Colombia. *Can J Forest Res*, **20**: 1583–1592.

Schimel JP, Firestone MK. 1989. Inorganic N incorporation by coniferous forest floor material. *Soil Biol and Biochem,* **21**: 41–46.

Strickland TC., Sollins p, Rudd N, and Schimel DS. 1992. Rapid stabilization and mobilization of ^{15}N in forest and range soils. *Soil Biol and Biochem*, **9**: 849–855.

Titema A, Wessel WW. 1992. Gross nitrogen transformations in the organic layer of acid forest ecosystems subjected to increased atmospheric nitrogen input. *Soil Biol and Biochem,* **24**: 943–950.

Vitousek PM, Matson PA. 1985. Disturbance, nitrogen availability, and nitrogen losses in an intensively managed loblolly pine plantation. *Ecology,* **66**: 1360–1376.

Wright RF, Van Breeman N. 1995. The Nitrex project: an introduction. *For Ecol and Manage*, **71**: 1–6.